

THE INTERACTIONS OF LITTORAL ZOOPLANKTON
AND THEIR FISH PREDATORS

By
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Abstract of Dissertation Presented to the
Graduate Council of the University of Florida in Partial Fulfillment
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THE INTERACTIONS OF LITTORAL ZOOPLANKTON
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Major Department: Zoology

The effects of environmental variables (temperature, primary productivity and lake level) on littoral zooplankton population dynamics and the influence of changes in zooplankton composition on the feeding habits of two species of littoral fishes were investigated. Zooplankton samples were taken from June, 1968, through April, 1970, in the littoral zone of two oligotrophic sandhills lakes in north-central Florida. Littoral zooplankters were identified and counted. Collections of Etheostoma fusiforme and Heterandria formosa were made in the same area as the plankton samples. The entire gut contents of both species of fishes were examined to determine the composition of the diet.

Simple and multiple correlation analyses were made between population density of certain species of zooplankton and environmental parameters. Electivity indices, gut clearance rate and predation pressure exerted by the fishes were calculated.

Of the environmental parameters examined, fluctuations in primary productivity and temperature had the greatest effect on population density. Population density of species of Chydoridae (Cladocera) which commonly inhabit littoral vegetation and species diversity of zooplankton were affected strongly by lake level fluctuations and the resultant changes in habitat diversity.

Electivity indices showed that size and accessibility were equally important factors in determining prey selection. The estimate of predation pressure indicated that predation by the two species of fishes was not an important factor controlling littoral zooplankton density.

INTRODUCTION

The littoral zone of a lacustrine ecosystem is characterized by an especially rich flora and fauna. It provides food and cover, as well as a site for reproduction for many species of animals. Unfortunately, the interrelationships of this zone are practically unknown. This study is concerned with the effects of environmental variables on the interactions of littoral zooplankton (Cladocera, Copepoda, Rotifera) and planktivorous fish.

The littoral zooplankton is quite variable with respect to its component species and to the presence of relatively many species as opposed to the limnetic zooplankton (Pennak, 1955). However, the ecology of littoral zooplankton is not well known (Harmsworth, 1968). Knowledge of the distribution of species of littoral Cladocera in the United States is based primarily on collections by Birge (1910) and a latitudinal transect in the Mississippi Valley by DeCosta (1964). DeCosta found climate to be a major factor limiting species distribution, but Smyly (1957), Quade (1969) and Whiteside (1970) suggested that distribution is correlated with the presence of suitable habitat.

The influence of environmental variables on seasonal succession of pond microcrustacea has been studied by Ward (1940), Smyly (1957) and Armitage and Davis (1967). Temperature and habitat were shown to be important factors.

Several investigators have used cladoceran microfossils in sediments, especially those of the Chydoridae, as indicators of lake history (Frey, 1961; Mueller, 1964; Goulden, 1964; Harmsworth, 1968). They have assumed that cladoceran abundance reflects actual changes in productivity during the ontogeny of lakes. Recently Harmsworth and Whiteside (1968) have presented evidence suggesting there is no relationship between cladoceran abundance and phytoplanktonic productivity, and thus no correlation between lake productivity and numbers of chydorid remains in sediments. They suggested instead that the dominant factor controlling the numbers of chydorids would be the extent of the littoral. Whiteside (1968) reported an inverse correlation between primary production and species diversity. This inverse relationship is common in other communities (Margalef, 1963).

Other workers have used Cladocera, especially the littoral species, as indicators of lake type (Hansen, 1961; Whiteside, 1970). From correlations between chydorids and physico-chemical properties of lakes, Whiteside (1970) suggested that most species prefer waters which are oligotrophic and dystrophic, while others typified eutrophic or polluted sites.

Predator-prey interactions in the limnetic zone have been examined. A classic study by Brooks and Dodson (1965) showed the effect of selective predation on zooplankton populations by a piscine planktivore. Similar studies have been conducted by Berg and Grimaldi (1966b), Galbraith (1967), Brooks (1968) and Dodson (1970). Such studies in the littoral zone have been limited to gut content analyses of game fish fry (Gerking, 1964; Chable, 1947). In general, these dealt with larger fry, which were no longer dependent on littoral zooplankton as a major food source.

I have studied the effects of temperature, primary productivity and lake level on the population dynamics of the littoral zooplankton, especially the chydorid Cladocera. By comparison of zooplankters in samples and in guts of fishes, factors important in influencing food selection have been examined. An incidental result of this research was the extension of ranges for certain chydorid species formerly thought to be more northern in distribution.

DESCRIPTION OF LAKES

The lakes chosen for the study, Anderson-Cue and McCloud, are oligotrophic sandhills lakes located about four miles east of Melrose in Putnam County, Florida. Both lakes are approximately the same size (twenty acres) and fifteen to twenty feet deep. They differ considerably in littoral development, McCloud's littoral being twenty to sixty feet wide and Anderson-Cue's being only fifteen to thirty feet wide. The extent of the littoral in both lakes fluctuates drastically with water level. The first year of the study (June, 1968, to May, 1969) was quite dry, resulting in a decrease in the littoral zone area. The second year (June, 1969, to April, 1970) had a very wet winter, returning the lake level to its early 1968 value.

Lake McCloud's littoral is divided into an inner zone and two outer zones separated by open water. Along the shore and shallows Hypericum myrtifolium and Cephalanthus occidentalis are common. Less numerous plants include Mayaca aubletii, Fleocharis acicularis, Panicum hemitonum, Brasenia schreberi, Sagittaria graminea and Nymphoides aquaticum. These are interspersed among the dominant plant, Leerzia hexandra, in water up to three feet deep. The two outer zones consist of broad bands of L. hexandra.

Plant diversity is approximately the same in Anderson-Cue. The plants are in two distinct zones. The inner zone (depth less than

three feet) consists of emergent L. hexandra and E. acicularis. On the bottom are Ericaulon compressum and M. aubletii and along the shore is a row of H. myrtifolium. In deeper water L. hexandra grows in dense mats with emergent shoots.

Species of fishes common to both lakes are the largemouth bass (Micropterus salmoides), the bluegill (Lepomis macrochirus), the warmouth (Chaenobryttus gulosus), the brook silversides (Labidesthes sicculus), the mosquito fish (Gambusia affinis), the least killifish (Heterandria formosa) and the eastern swamp darter (Etheostoma fusiforme). Two species found only in Lake McCloud are the golden topminnow (Fundulus chrysotus) and the starhead topminnow (Fundulus lineolatus).

These lakes are also being used in a study on eutrophication conducted by the Department of Environmental Engineering (Brezonik et al., 1969). Lake Anderson-Cue has been receiving a controlled flow of secondary sewage effluent enriched with NH_4Cl and Na_3PO_4 since March, 1967. The nutrient addition rates are comparable to those estimated for the nutrient budget of Lake Mendota, Wisconsin, by Lee et al. (1966). Lake McCloud, similar in biological and chemical characteristics, is the control. Measurements of temperature, limnetic primary productivity and lake level were made available to me by the Department of Environmental Engineering.

MATERIALS AND METHODS

Sampling

Zooplankton collections were made in each lake every two weeks. Samples were taken in the inner zone (water depth = 0.5 - 1.0 m) with a Van Dorn water sampler (volume = 1.93 l) after vigorous stirring to dislodge organisms from the vegetation and insure random dispersal in the water column. These were concentrated to 32 ml with a plankton net and preserved in 1 percent formalin. Three one-ml aliquots were counted. All Cladocera were identified to species. Rotifera were identified to genus. Copepoda and their nauplii were counted, but not identified. Counts were converted to organisms per m^2 by multiplying the organisms per m^3 by the depth (m) at the sampling site.

Etheostoma fusiforme and Heterandria formosa were collected every two weeks with a dipnet in the same area as the plankton sample. Five fish of each species were taken from each lake and preserved in 10 percent formalin. Due to the small size of the fishes and the lack of a definitive stomach in H. formosa, the entire gut contents were removed and counted. Although total length of each fish examined was recorded, all sizes of both species of fishes fed on the same organisms.

The contribution of each species or group of zooplankters to the diet was expressed as its percentage of the total organisms eaten. Due to the large number of species and the difficulty in measuring the biomass

of individual zooplankters, the contribution of species or groups in terms of proportion of total biomass was not determined. Biweekly fish gut analyses were pooled and reported as monthly averages.

During the second year of the study, fish densities were estimated by pulling a wire mesh dredge through specified areas in the littoral at various times during the year.

Gut Clearance Rate

Laboratory experiments were conducted to determine gut clearance time at 15°C, 20°C and 30°C for both fishes. Following two weeks of acclimation fish were placed in a feeding chamber containing zooplankton. After 30 minutes they were returned to their original aquaria. At intervals of 1 or 1/2 hour, 5 fish were removed and their gut contents were examined, until the microorganisms were in the lower portion of the gut and were no longer identifiable.

RESULTS

Population Density

Table 1 shows species seen in littoral plankton samples from Lakes Anderson-Cue and McCloud during the two sampling years. Bosmina coregoni, Diaphanosoma brachyurum, Brachionus sp., Conochiloides sp., Keratella americana and K. taurocephala are more commonly found in the limnetic zone of both lakes (Maslin, 1969).

Figures 1 - 6 show changes in species composition and abundance in Anderson-Cue and McCloud from June, 1968, to April, 1970. In both lakes Copepoda and Rotifera were rarely absent from the plankton. The greatest seasonal changes in abundance were among the Cladocera. Chydorus sphaericus, Alona quadrangularis and Pleuroxus striatus were present in Anderson-Cue through most of the 1968-1969 sampling year. Other species, particularly Alona costata, A. rectangula and Alonella globulosa, had high densities June through August and/or January through May and were inabundant or absent during the fall. Of the species present from September through December, all showed decreased population levels.

In Lake McCloud only A. quadrangularis was present all year. Ilyocryptus spinifer was present from October through February. Most species were present June through August and/or January through May.

TABLE 1

Species of Zooplankton Present in Lakes Anderson-Cue and McCloud.

ORGANISM	Anderson-Cue	McCloud
Cladocera		
<u>Acantholeberis curvirostris</u>	X	X
<u>Acroperus harpae</u>	X	X
<u>Anchistropus minor</u>		X
<u>Alona affinis</u>	X	X
<u>A. costata</u>	X	X
<u>A. guttata</u>	X	X
<u>A. karua</u>	X	
<u>A. rectangula</u>	X	X
<u>A. quadrangularis</u>	X	X
<u>Alonella globulosa</u>	X	X
<u>Bosmina coregoni</u>	X	X
<u>Camptocercus rectirostris</u>	X	X
<u>Chydorus barroisi</u>		X
<u>C. bicornutus*</u>		X
<u>C. piger*</u>	X	X
<u>C. sphaericus</u>	X	X
<u>Diaphanosoma brachyurum</u>	X	X
<u>Eurycercus lamellatus</u>		X
<u>Graptoleberis testudinaria</u>	X	X
<u>Ilyocryptus spinifer</u>	X	X

*New record for southern United States.

TABLE 1 (cont.)

Species of Zooplankton Present in Lakes Anderson-Cue and McCloud.

ORGANISM	Anderson-Cue	McCloud
Cladocera (cont.)		
<u>Macrothrix rosea</u>	X	
<u>Pleuroxus striatus</u>	X	X
<u>Simocephalus exspinosus</u>	X	X
Rotifera		
<u>Brachionus</u> sp.	X	X
<u>Conochiloides</u> sp.		X
<u>Keratella americana</u>	X	X
<u>K. serrulata</u>	X	X
<u>K. taurocephala</u>	X	X
<u>Lecane</u> spp.	X	X
<u>Macrochaetus</u> sp.	X	X
<u>Monommata</u> sp.	X	X
<u>Monostyla</u> sp.	X	X
<u>Trichocerca</u> sp.	X	X
Copepoda		
<u>Cyclops exilis</u>	X	X
<u>Eucyclops speratus</u>	X	X

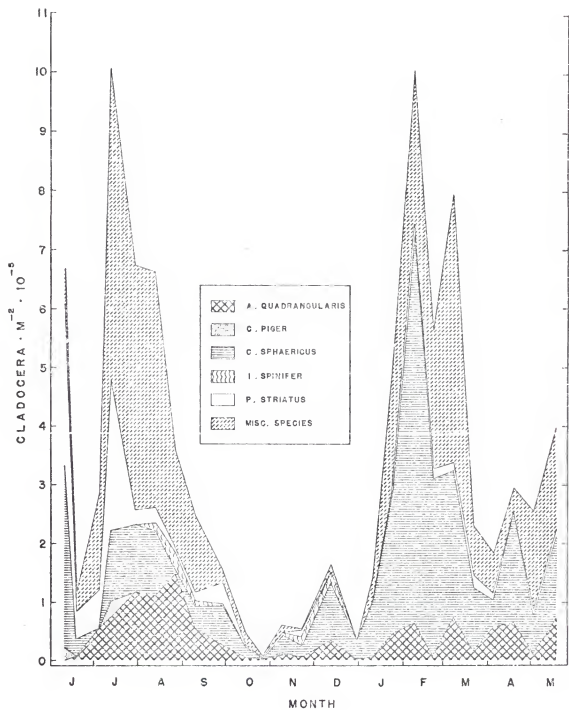


Figure 1. Changes in littoral cladoceran species composition and abundance in Lake Anderson-Cue, 1968-1969. (Pattern width on any given date indicates the density of the corresponding species.)

Figure 2. Changes in littoral cladoceran species composition and abundance in Lake Anderson-Cue, 1969-1970. (Pattern width on any given date indicates the density of the corresponding species.)

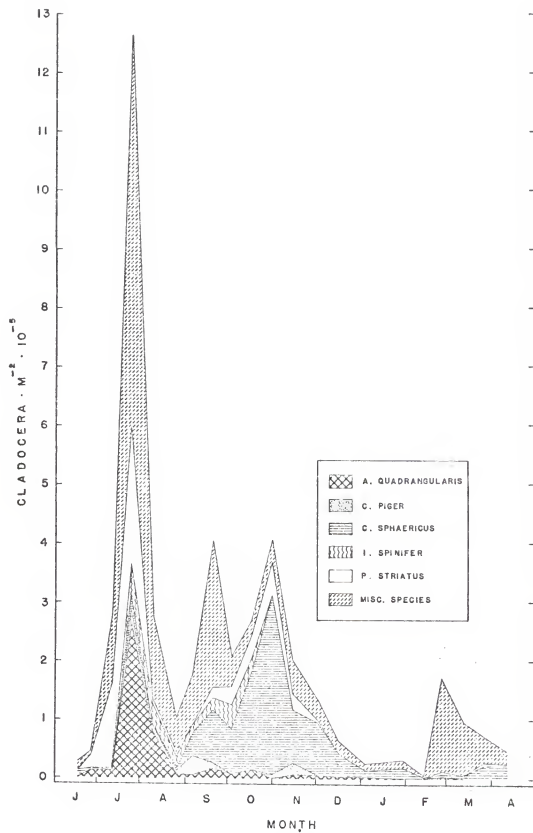


Figure 3. Changes in littoral cladoceran species composition and abundance in Lake McCloud, 1968-1969. (Pattern width on any given date indicates the density of the corresponding species.)

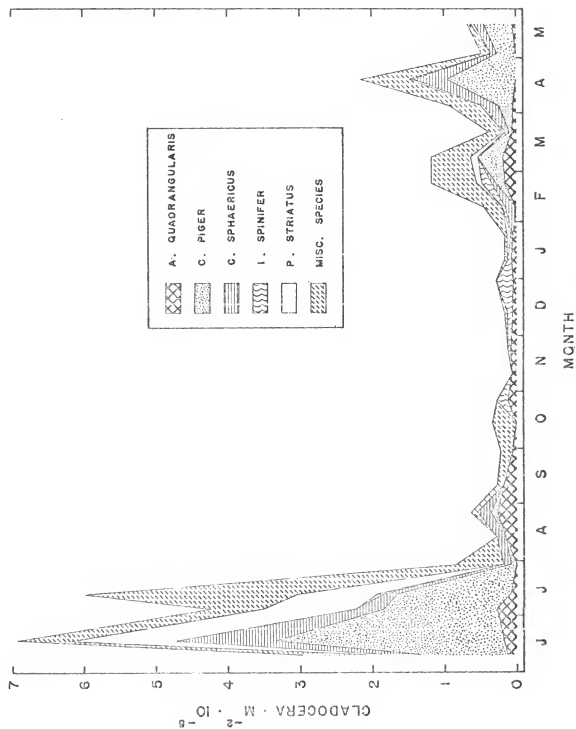


Figure 4. Changes in littoral cladoceran species composition and abundance in Lake McCloud, 1969-1970. (Pattern on any given date indicates the density of the corresponding species.)

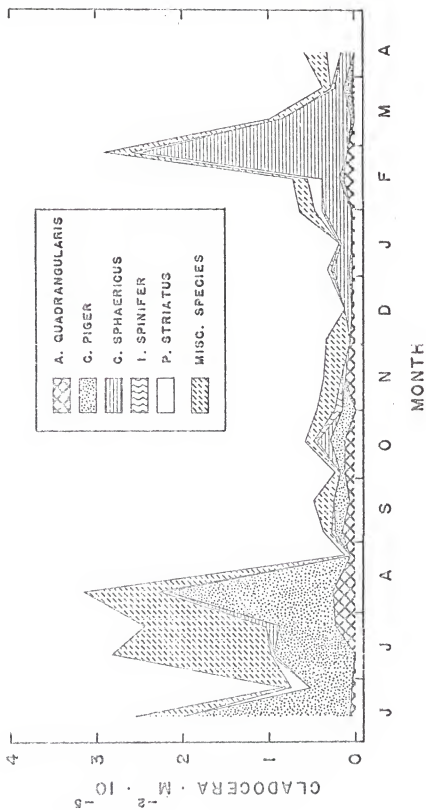
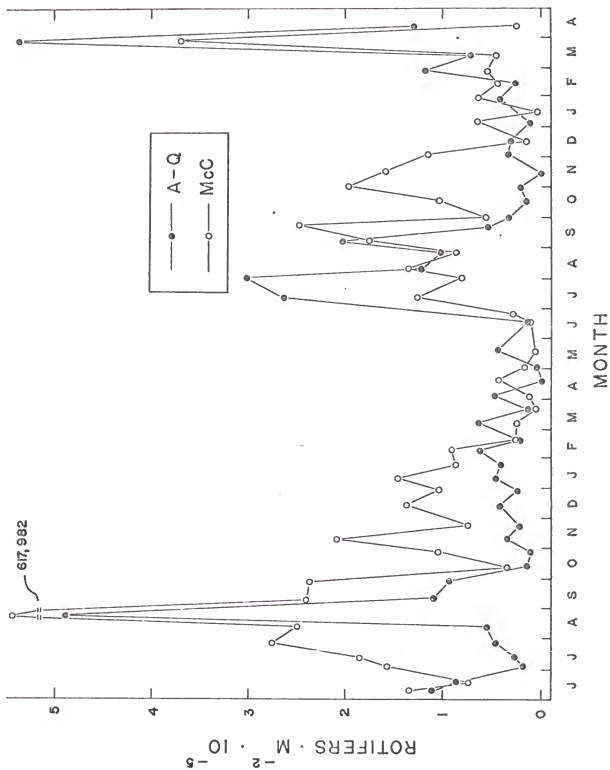


Figure 5. Fluctuations in littoral Copepoda populations in
Anderson-Cue and McCloud, 1968-1970.

Figure 6. Fluctuations in littoral Rotifera populations in
Anderson-Gue and McCloud, 1968-1970.



In Anderson-Cue, 1969-1970, the four species of Cladocera present most of the year were C. sphaericus, A. quadrangularis, P. striatus and Acroperus harpae. All chydorids except C. sphaericus and Graptoleberis testudinaria were less abundant from mid-October through March than during the summer. Common limnetic species, B. coregoni and Keratella spp. (Rotifera), were quite numerous during February and March. B. coregoni reached a density of 141,000 organisms per m².

In Lake McCloud, 1969-1970, the pattern of species composition was very similar to the previous year, with the exception of C. sphaericus, which was present October through January. Two species of Rotifera, Brachionus sp. and Monommata sp., developed populations during this period and continued to be numerous January through March. Keratella spp. and Conochiloides sp., commonly limnetic, were abundant January through March, but were not present during the same period of the previous year.

Relationship of Littoral Zooplankton to Environmental Parameters

Three factors which may influence littoral zooplankton populations are primary productivity, temperature and lake level. Figures 7 and 8 show changes in these parameters during the study period. Temperatures in the two lakes were approximately the same and only the data for Lake McCloud are presented. Lake level changes were measured only for Anderson-Cue, but both lakes fluctuated similarly.

Table 2 shows correlation coefficients between littoral zooplankton populations and environmental parameters. Total zooplankton was significantly correlated ($p = 0.05$) with temperature in Anderson-Cue, 1968-1969. This was primarily due to the high correlation of copepods and temperature, since copepods generally made up a large percentage of the zooplankton.

Figure 7. Variation in primary productivity in Anderson-Cue
and McCloud, 1968-1970.

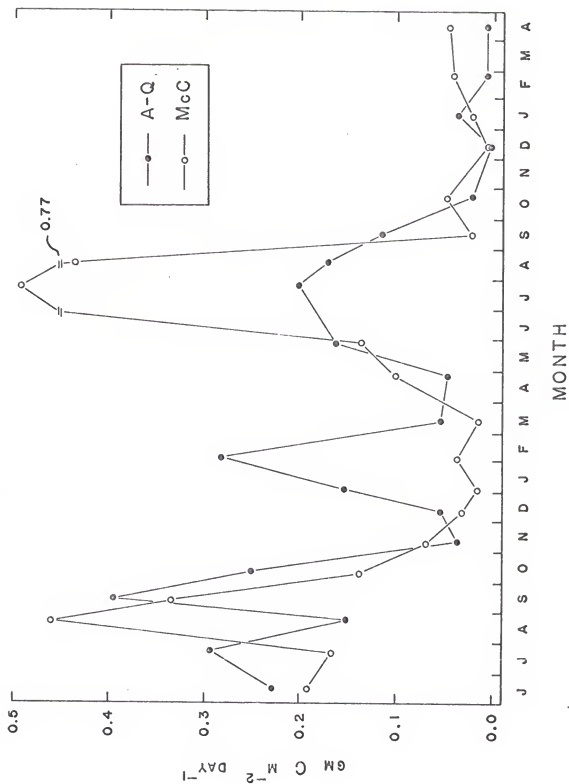


Figure 8. Variation in temperature in Lake McCloud and lake level - mean sea level in Lake Anderson-Cue, 1968-1970.

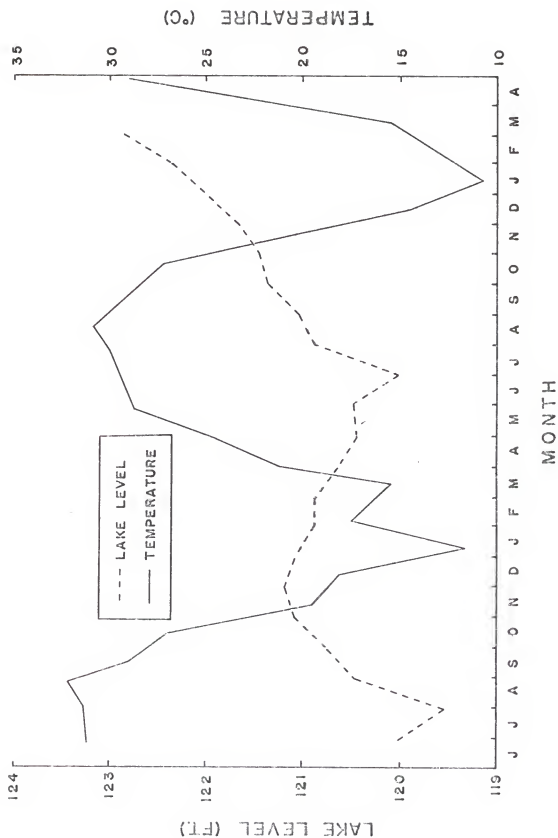


TABLE 2

Correlation of Littoral Zooplankton to Temperature and Primary Productivity.

	Lake Anderson-Cue				Lake McCloud			
	1968-1969		1969-1970		1968-1969		1969-1970	
	temp.	prod.	temp.	prod.	temp.	prod.	temp.	prod.
Total Zooplankton	0.519*	0.457*	0.377	0.357	0.768*	0.624*	0.504*	0.425
Cladocera	0.188	0.441	0.442	0.386	0.393	0.137	0.470*	0.830*
Copepoda	0.583*	0.434	0.428	0.375	0.818*	0.714*	0.404	-0.053
Rotifera	0.344	0.057	0.537*	0.783*	0.519*	0.794*	0.414	-0.034
Cladocera	1968-1969(- fall)		1969-1970(- fall)		1968-1969(- fall)		1969-1970(- fall)	
	0.106	0.598*	0.453	0.486	0.489*	0.163	0.519*	0.666*

*Significant at the 0.05 level.

In 1969-1970 total zooplankton was not strongly correlated with temperature or primary productivity, but showed the same trend as the previous year. Copepoda and Cladocera were correlated with temperature, but Rotifera were more strongly correlated with primary productivity.

In McCloud, 1968-1969, total zooplankton was highly correlated with temperature and primary productivity. These two factors were also highly correlated with each other ($r = 0.847$, $p = 0.001$). Temperature seemed more important for Cladocera and Copepoda, while primary productivity were more important for Rotifera.

In 1969-1970 total zooplankton was again better correlated with temperature. However, Cladocera were highly correlated with primary productivity. Copepoda and Rotifera were better correlated with temperature, but not highly. Temperature and primary productivity were not as well correlated ($r = 0.601$, $p = 0.05$).

Total cladoceran density was not strongly correlated with the environmental parameters. This was primarily due to the absence or reduced population density of most species from September through December. Correlations between total cladoceran density, primary productivity and temperature were run excluding the period from September through December. All correlation coefficients were higher, except the value for McCloud, 1969-1970. This suggested that while primary productivity and temperature were important most of the year, some other factor was influencing population density in the fall.

Lake level fluctuation was also considered, but no group or individual species was significantly correlated with it.

In order to rate the environmental variables in order of their importance, a multiple linear regression analysis was conducted using

primary productivity, temperature and lake level as independent variables and population density of C. sphaericus, Lecane spp. and total Copepoda as dependent variables for Lake Anderson-Cue. Due to the irregularity of Cladocera in Lake McCloud, only Lecane spp. and total Copepoda were considered. Species chosen were those present most of the time. The results are summarized in Table 3. F ratios were tested at $p = 0.05$ level of significance. R^2 , the coefficient of concordance, is the fraction of the sum of squares of deviations of the dependent variables from its mean that is attributable to the regression. The variable giving the greatest increase in the value of R^2 is the most important of the three considered.

Temperature was the most important variable for C. sphaericus populations. Of the three significant values, Lecane populations were best correlated with primary productivity. Copepods were significantly correlated with these three variables only once.

Species Diversity

Species diversity can be measured in many ways. One method commonly used is according to the equation by Shannon (1949):

$$D = \sum_{i=1}^m P_i \log_2 P_i$$

where P_i = the probability of occurrence of the i th species. This method takes into account the number of individuals within a sample as well as the number of species. The results are summarized in Table 4. The mean species diversities in the two lakes for the complete year were

TABLE 3

Relationship of Littoral Zooplankton to Primary Production (P),
Temperature (T) and Lake Level (L).

Organism	F ratio	Environmental Variable	R ²	Increase in R ²
Lake Anderson-Cue, 1968-1969				
<u>C. sphaericus</u>	6.673*	P	0.0001	0.0001
		P+T	0.4610	0.4609
		P+T+L	0.4880	0.0270
<u>Lecane</u> spp.	1.991	P	0.0283	0.0283
		P+T	0.1083	0.0800
		P+T+L	0.2214	0.1132
Copepoda	2.650	P	0.0647	0.0647
		P+T	0.0743	0.0096
		P+T+L	0.2746	0.2003
Lake McCloud, 1968-1969				
<u>Lecane</u> spp.	27.156*	P	0.6107	0.6107
		P+T	0.7180	0.1073
		P+T+L	0.7951	0.0771
Copepoda	1.084	P	0.0821	0.0821
		P+T	0.1213	0.0392
		P+T+L	0.1340	0.0127
Lake Anderson-Cue, 1969-1970				
<u>C. sphaericus</u>	17.192*	P	0.1841	0.1841
		P+T	0.7347	0.5506
		P+T+L	0.7865	0.0518
<u>Lecane</u> spp.	5.676*	P	0.5323	0.5323
		P+T	0.5413	0.0091
		P+T+L	0.5488	0.0075
Copepoda	1.964	P	0.2052	0.2052
		P+T	0.2657	0.0605
		P+T+L	0.2962	0.0305
Lake McCloud, 1969-1970				
<u>Lecane</u> spp.	5.182*	P	0.2719	0.2719
		P+T	0.4123	0.1404
		P+T+L	0.5089	0.0966
Copepoda	5.395*	P	0.1063	0.1063
		P+T	0.4568	0.3505
		P+T+L	0.5190	0.0622

*Significant at the 0.05 level.

TABLE 4

Species Diversity of Littoral Zooplankton.

	Lake Anderson-Cue		Lake McCloud
1968-1969			
Total year	2.2163 ± 0.1533	Total year	1.9677 ± 0.2154
Jun - Aug	2.3432 ± 0.3856	Jun - Aug	2.1215 ± 0.3751
Sep - Dec	$1.9329^{*\pm} 0.2360$	Sep - Dec	$1.4220^{*\pm} 0.2081$
Jan - May	2.3542 ± 0.2094	Jan - May	2.2667 ± 0.2680
1969-1970			
Total year	2.1279 ± 0.2279	Total year	1.9798 ± 0.2346
Jun - 3 Oct	2.4359 ± 0.1743	Jun - Sep	2.2562 ± 0.3306
17 Oct - Mar	$1.8760^{*\pm} 0.3388$	Oct - 15 Jan	$1.5377^{*\pm} 0.3459$
		29 Jan - Mar	2.2449 ± 0.4530

*Significantly different from other values at the 0.05 level.

compared using Student's t test and were not statistically different from one another at the 0.05 level. Both years were then divided into segments where there seemed to be a distinct change in the trend of the values.

Species diversity was high in the summer and spring with a period of lowered diversity in the fall. This pattern was similar in Lake McCloud both sampling years and in Anderson-Cue in 1968-1969. Anderson-Cue did not show a return to a higher value in the spring of 1969-1970.

Diet and Zooplankton Composition

Figures 9 - 20 show the changes in contributions of the major groups to the total zooplankton and the accompanying changes in the diet of E. fusiforme and H. formosa. The component of nonplankters (insect larvae, amphipods, ostracods, etc.) is indicated, although it was not counted in the plankton sample.

Table 5 summarizes the data shown in Figures 9 - 20.

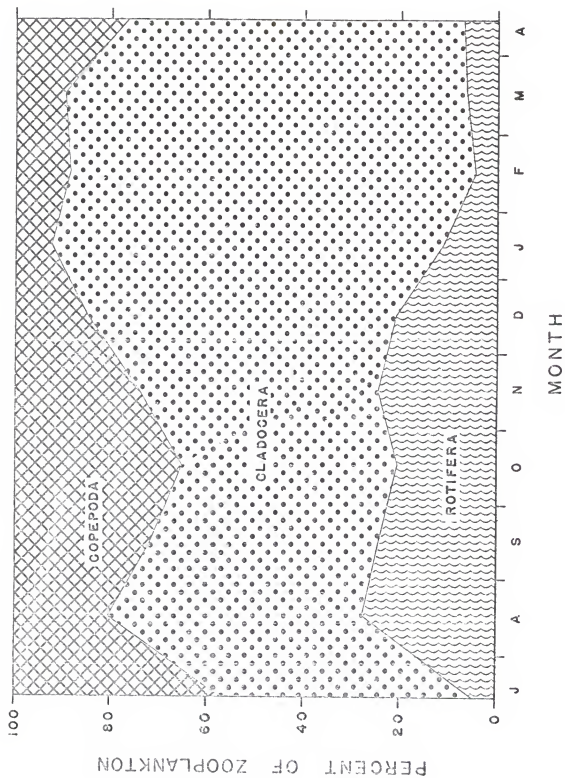
TABLE 5

Mean Percentages of Organisms Eaten by E. fusiforme and H. formosa.

Organism	<u>E. fusiforme</u>		<u>H. formosa</u>	
	A-Q	McC	A-Q	McC
Cladocera	82.9	50.6	68.5	38.3
Copepoda	6.9	30.9	6.0	14.3
Rotifera	1.0	1.6	20.8	36.3
Nonplankters	6.9	16.7	2.8	9.9

Figure 9. Seasonal fluctuations in littoral zooplankton in Anderson-Cue, 1968-1969. (Width of pattern represents the percent of the total zooplankton comprised by each group. Percents are monthly averages. This also refers to Figures 12, 15 and 18.)

Figure 10. Seasonal fluctuations in the diet of E. fusiforme
in Anderson-Cue, 1968-1969. (Width of pattern
indicates the fraction of total organisms eaten
comprised by each group. Percents are monthly averages.
This also refers to Figures 11, 13, 14, 16, 17, 19 and 20.)



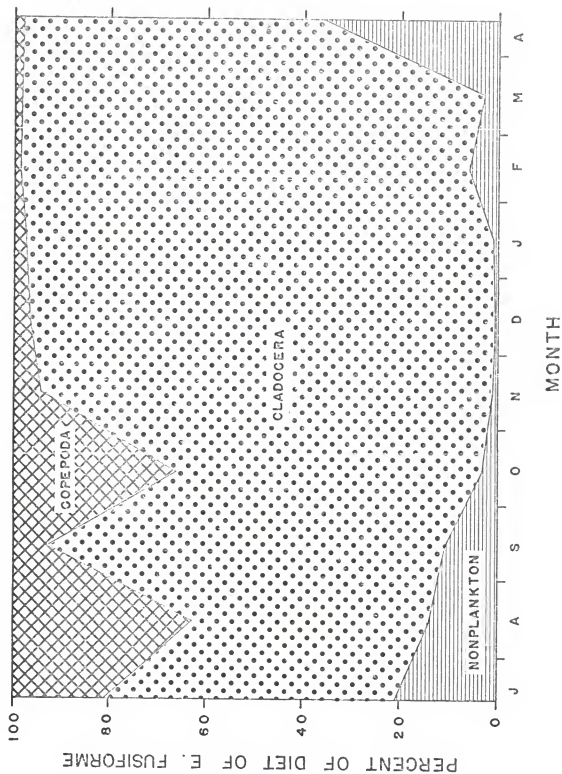


Figure 11. Seasonal fluctuations in the diet of H. formosa
in Anderson-Cue, 1968-1969.

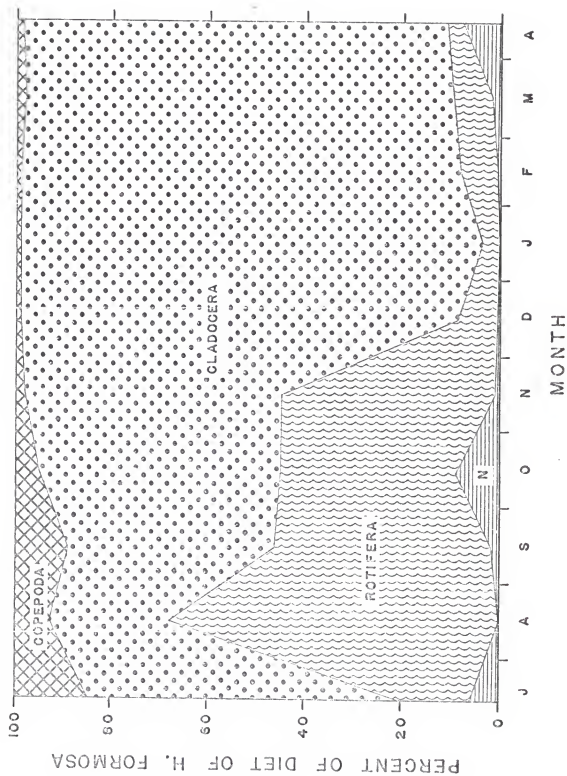


Figure 12. Seasonal fluctuations in littoral zooplankton
in McCloud, 1968-1969.

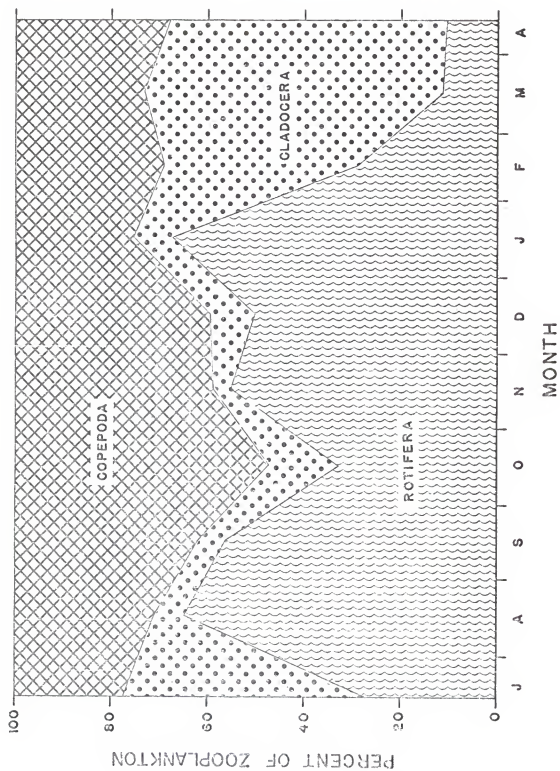


Figure 13. Seasonal fluctuations in the diet of E. fusiforme
in McCloud, 1968-1969.

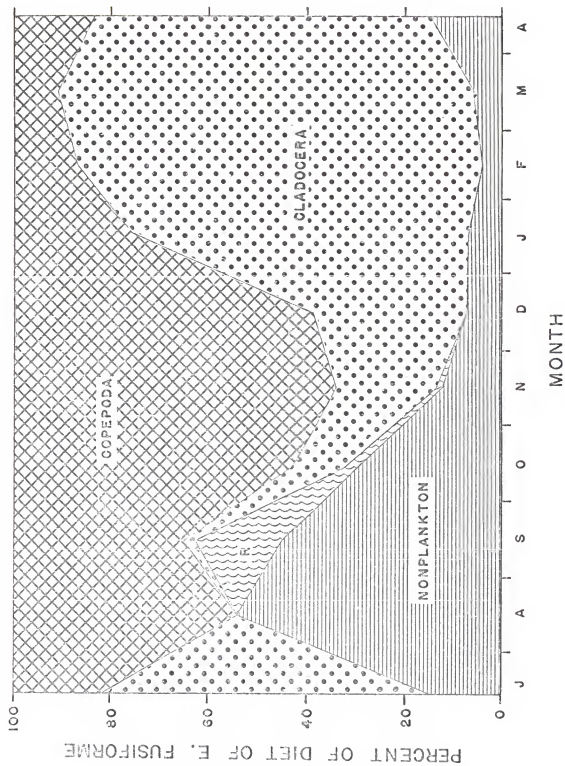


Figure 14. Seasonal fluctuations in the diet of H. formosa
in McCloud, 1968-1969.

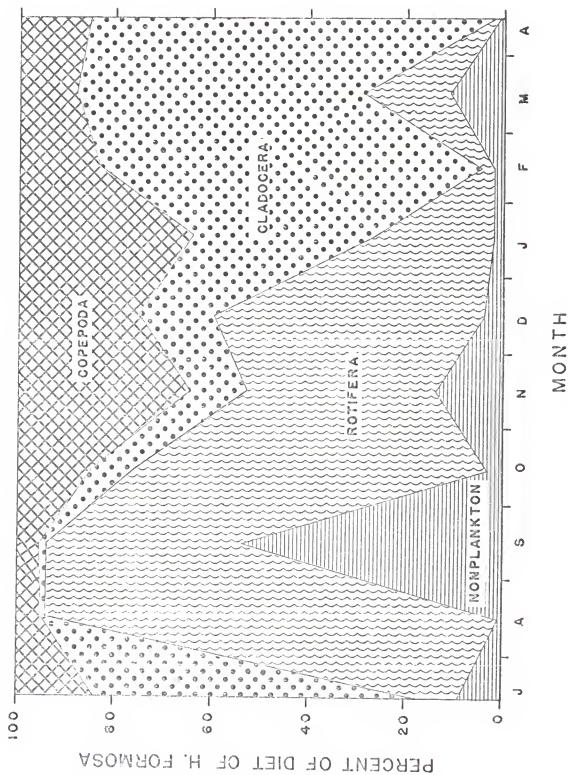


Figure 15. Seasonal fluctuations in littoral zooplankton in
Anderson-Cue, 1969-1970.

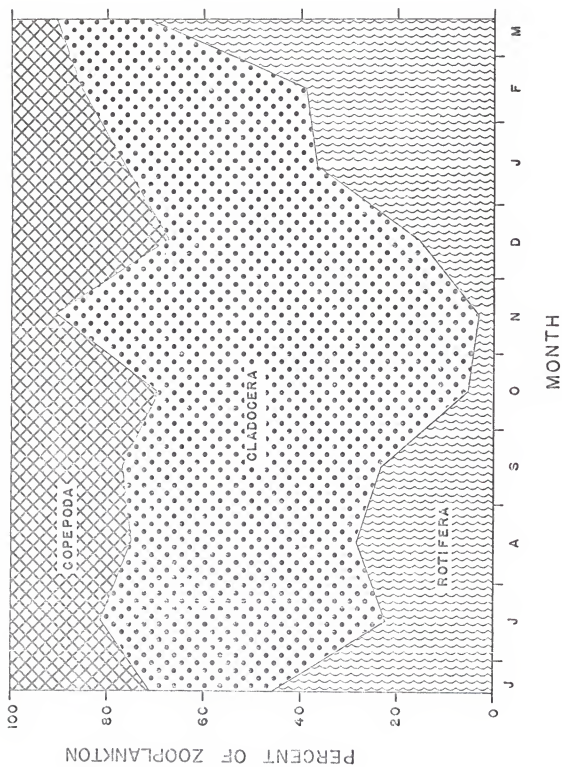


Figure 16. Seasonal fluctuations in the diet of E. fusiforme in
Anderson-Cue, 1969-1970.

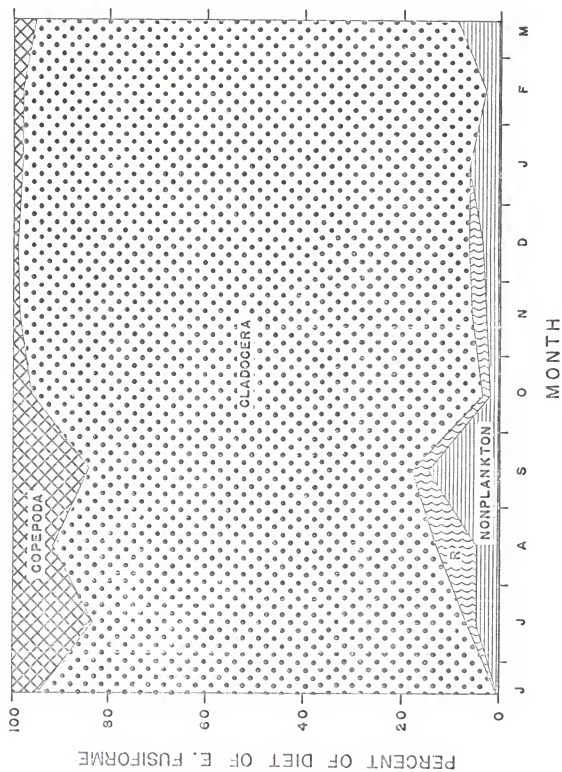


Figure 17. Seasonal fluctuations in the diet of H. formosa in
Anderson-Cue, 1969-1970.

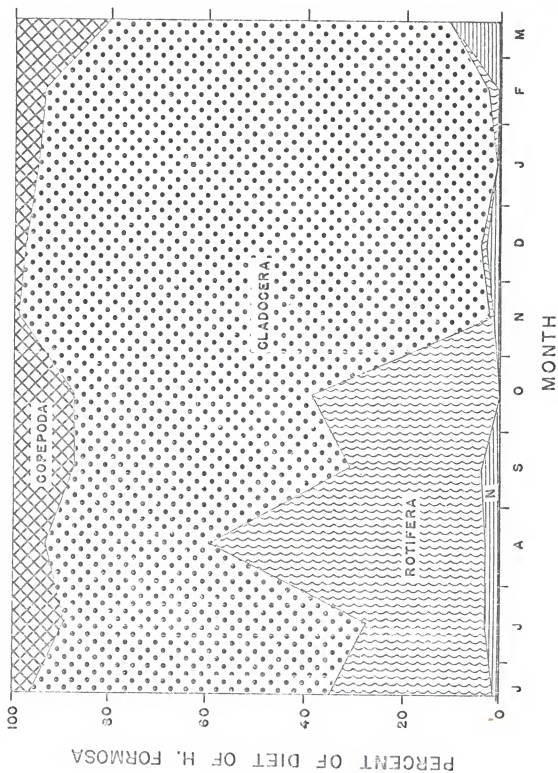


Figure 18. Seasonal fluctuations in littoral zooplankton in
McCloud, 1969-1970.

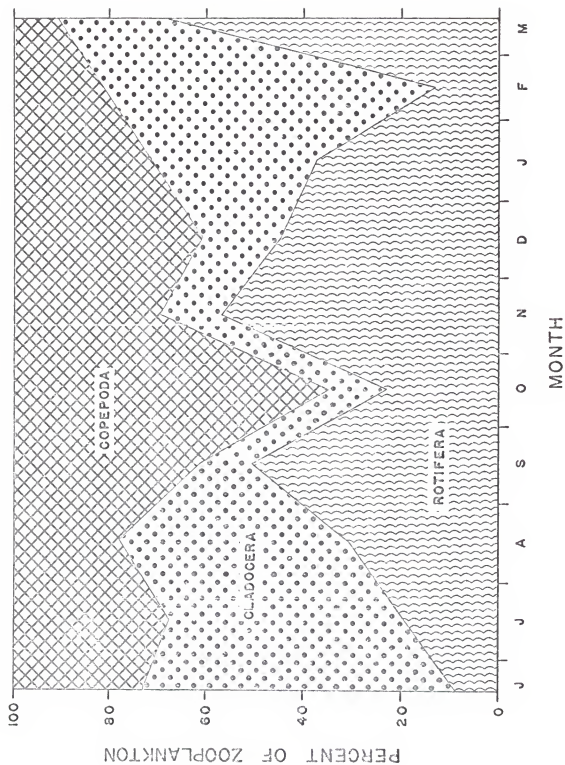


Figure 19. Seasonal fluctuations in the diet of E. fusiforme in
McCloud, 1969-1970.

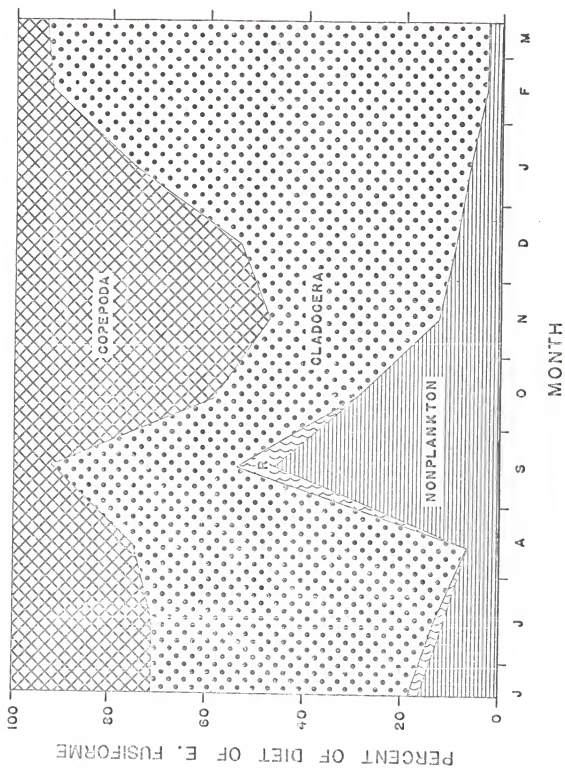
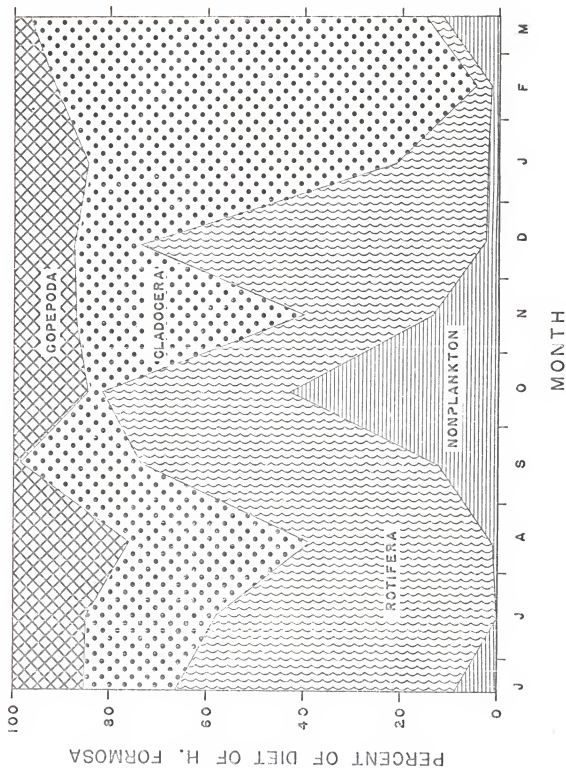


Figure 20. Seasonal fluctuations in the diet of H. formosa in
McCloud, 1969-1970.



As shown in Table 5 and Figures 9 - 20, the diet of E. fusiforme was very different in the two lakes, mainly because of the low percentage of Cladocera in Lake McCloud during the fall. Nonplankton was important, even when Cladocera were abundant. More nonplankton was eaten in McCloud than in Anderson-Cue. More copepods were eaten when Cladocera and nonplankton were not abundant in the littoral. Rotifers were rarely eaten, although the gill raker spacings of E. fusiforme are obviously small enough to retain them.

The differences in diet of H. formosa in the two lakes were also attributable to differences in cladoceran populations. Rotifera were very important items of the diet in the fall, when Cladocera were scarce. More nonplankton was eaten in Lake McCloud than in Anderson-Cue, but usually when Rotifera were not abundant. Copepods seemed to be important only when other groups were scarce.

Both fishes depended on Cladocera when they were present so that the component of Cladocera in the diet was disproportionately large compared to the plankton. In Anderson-Cue Cladocera averaged 56.1 percent of the zooplankton, while they were 82.9 percent of the diet of E. fusiforme and 68.5 percent of the diet of H. formosa. In McCloud Cladocera averaged 29.7 percent of the zooplankton, 50.6 percent of the diet of E. fusiforme and 38.3 percent of the diet of H. formosa. In the absence of Cladocera, E. fusiforme ate nonplankton and copepods, while H. formosa ate rotifers. This pattern of resource partitioning was quite similar in both lakes for both years. Cladoceran abundance was not as low in Anderson-Cue, but the variance in the C. sphaericus population produced the same changes in diet. Limnetic rotifers, which were abundant in the littoral of both lakes in the spring, 1970, were rarely eaten.

E. fusiforme is reported to live on the bottom of lakes, in shallows and open water (McLane, 1955). However, because of the similarity in the species of Cladocera eaten and the fact that E. fusiforme ate planktonic copepods, it appeared that both fishes were feeding throughout the water column (depth = 0.5 - 1.0 m).

Prey Selection

Tables 6 and 7 show mean electivity indices for each organism. These were calculated using the formula adopted by Ivlev (1961):

$$E = \frac{r_i - p_i}{r_i + p_i}$$

where r_i = the ratio of any organism in the ration and p_i = the ratio of the same organism in the food complex of the environment. Values of E range from - 1 to + 1, with zero meaning "eaten at random."

E. fusiforme generally had higher electivity indices than H. formosa for A. curvirostris, A. harpae, A. affinis, A. quadrangularis, C. piger, E. lamellatus, G. testudinaria and S. exspinosus.

Table 8 shows the mean percentages of cladoceran species in the diet of the two fishes. C. sphaericus was the most important cladoceran in the diet of both fishes in Anderson-Cue. A. curvirostris, A. harpae, A. affinis and A. quadrangularis made up a larger percent of the diet of E. fusiforme than of H. formosa.

TABLE 6

Mean Electivity Indices for E. fusiforme and H. formosa in Lake Anderson-Cue.

Organism	<u>E. fusiforme</u>		<u>H. formosa</u>	
	1968-1969	1969-1970	1968-1969	1969-1970
<u>A. curvirostris</u>	+0.34	+0.31	+0.26	+0.20
<u>A. harpae</u>	+0.30	+0.59	0.00	-0.43
<u>A. affinis</u>	+0.13	+0.79	-0.35	+0.41
<u>A. guttata</u>	-0.87	-0.40	-0.62	-0.40
<u>A. quadrangularis</u>	-0.16	+0.14	-0.19	-0.08
<u>A. globulosa</u>	+0.01	-0.13	+0.10	-0.22
<u>B. coregoni</u>	---	+0.14	---	-0.10
<u>C. rectirostris</u>	-0.03	+0.47	-0.01	+0.47
<u>C. piger</u>	-0.02	+0.05	-0.20	-0.40
<u>C. sphaericus</u>	+0.38	+0.62	+0.38	+0.49
<u>D. brachyurum</u>	---	-0.03	---	-0.12
<u>G. testudinaria</u>	-0.05	+0.28	+0.02	+0.21
<u>I. spinifer</u>	-0.15	-0.09	+0.03	-0.03
<u>M. rosea</u>	-0.22	+0.58	-0.19	+0.32
<u>P. striatus</u>	-0.52	-0.55	-0.07	-0.30
<u>S. exspinosus</u>	+0.20	+0.34	---	-0.01
<u>Lecane spp.</u>	-1.00	-0.51	+0.04	-0.16
<u>Monostyla sp.</u>	-0.90	-0.78	+0.37	-0.18
<u>Trichocerca sp.</u>	-0.40	+0.10	-0.18	+0.10
Copepoda	-0.32	-0.53	-0.61	-0.36
Nauplii	-0.97	-0.90	-0.90	-0.84

TABLE 7

Mean Electivity Indices for E. fusiforme and H. formosa in Lake McCloud.

Organism	<u>E. fusiforme</u>		<u>H. formosa</u>	
	1968-1969	1969-1970	1968-1969	1969-1970
<u>A. curvirostris</u>	+0.34	+0.39	+0.35	+0.21
<u>A. harpae</u>	---	+0.30	---	0.00
<u>A. affinis</u>	+0.14	+0.48	-0.06	+0.24
<u>A. guttata</u>	-0.53	-0.30	-0.25	-0.27
<u>A. quadrangularis</u>	+0.27	+0.23	+0.11	+0.13
<u>A. globulosa</u>	0.00	+0.02	+0.09	-0.10
<u>B. coregoni</u>	---	+0.10	---	+0.20
<u>C. rectirostris</u>	+0.23	+0.43	+0.41	+0.21
<u>C. piger</u>	+0.16	+0.32	-0.11	-0.21
<u>C. sphaericus</u>	-0.04	+0.24	+0.17	+0.31
<u>D. brachyurum</u>	---	-0.10	---	-0.41
<u>E. lamellatus</u>	+0.55	---	-0.08	---
<u>G. testudinaria</u>	+0.22	+0.03	+0.04	-0.22
<u>I. spinifer</u>	-0.41	-0.20	-0.27	-0.31
<u>M. rosea</u>	+0.20	+0.30	+0.10	+0.10
<u>P. striatus</u>	-0.05	+0.02	+0.18	-0.03
<u>S. exspinosus</u>	-0.10	+0.66	-0.20	-0.13
<u>Lecane spp.</u>	-0.81	-0.83	-0.29	+0.27
<u>Monostyla sp.</u>	-0.80	-1.00	+0.27	+0.22
<u>Trichocerca sp.</u>	---	-0.80	+0.33	-0.50
Copepoda	+0.18	+0.05	-0.22	-0.33
Nauplii	-1.00	-1.00	-0.90	-0.87

TABLE 8

Mean Percentages of Cladoceran Species in the Diet of E. fusiforme
and H. formosa

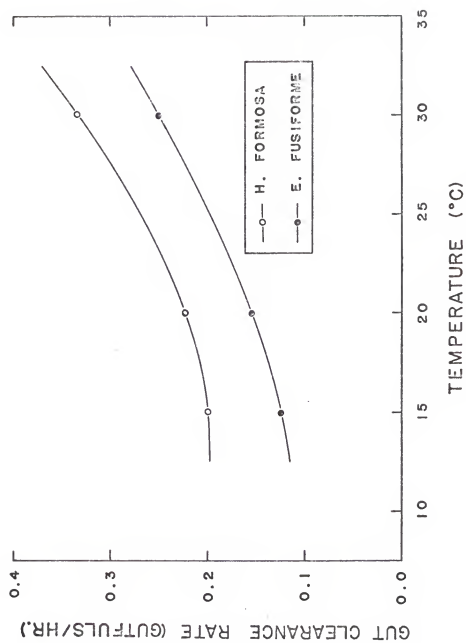
Species	<u>E. fusiforme</u>		<u>H. formosa</u>	
	<u>A-Q</u>	<u>McC</u>	<u>A-Q</u>	<u>McC</u>
<u>A. curvirostris</u>	8.0	9.0	3.5	5.5
<u>A. harpae</u>	4.2	0.1	0.3	0.0
<u>A. affinis</u>	5.8	3.6	1.9	1.4
<u>A. guttata</u>	0.1	0.1	0.5	0.7
<u>A. quadrangularis</u>	4.5	6.6	3.6	3.6
<u>A. globulosa</u>	2.5	0.7	3.5	1.7
<u>C. rectirostris</u>	0.4	1.1	0.4	0.9
<u>C. piger</u>	0.2	6.3	0.0	3.9
<u>C. sphaericus</u>	39.5	9.0	44.0	13.4
<u>G. testudinaria</u>	1.4	0.9	2.4	0.6
<u>I. spinifer</u>	6.5	3.3	1.4	1.2
<u>M. rosea</u>	2.0	0.4	2.0	0.6
<u>P. striatus</u>	0.8	1.2	1.9	1.2
<u>S. exspinosus</u>	4.9	5.2	0.6	0.9

TABLE 9

Densities (fish/m²) of E. fusiforme and H. formosa in the Littoral of Lakes Anderson-Cue and McCloud.

Date	<u>E. fusiforme</u>		<u>H. formosa</u>	
	<u>A-Q</u>	<u>McC</u>	<u>A-Q</u>	<u>McC</u>
18 April 1969	2.9	1.3	3.9	9.0
25 July 1969	4.6	2.6	2.4	10.1
31 October 1969	2.3	0.8	2.2	8.5
12 February 1970	2.9	0.8	0.0	0.9
26 April 1970	0.2	0.1	0.0	5.6
22 May 1970	2.4	0.5	0.1	6.7

Figure 21. Effect of temperature on gut clearance rate in
E. fusiforme and H. formosa.



Predation Pressure

Table 9 shows the changes in density of *E. fusiforme* and *H. formosa* during 1969-1970 in the same area where plankton samples were collected. Differences in fish densities probably resulted from seasonal habitat changes due to lake level fluctuations and migration, as well as actual changes in the overall populations.

Figure 21 shows the change in gut clearance rate (GCR) with temperature. The gut clearance rate, the reciprocal of gut clearance time, is the number of gutfuls of plankton which can be digested in an hour. The average daily ration of plankters for *E. fusiforme* and *H. formosa* was determined using mean temperature and daylength. Gut analyses of fish collected at night established that both species feed only during the day.

- 1.) $\frac{\text{average plankters}}{\text{gutful}} \times \text{GCR} \times \frac{\text{hours}}{\text{day}} = \frac{\text{plankters removed}}{\text{fish} \cdot \text{day}}$
- 2.) $\frac{\text{plankters removed}}{\text{fish} \cdot \text{day}} \times \frac{\text{fish}}{\text{m}^2} = \frac{\text{plankters removed}}{\text{day} \cdot \text{m}^2}$
- 3.) $\frac{\text{plankters removed}}{\text{day} \cdot \text{m}^2} \div \frac{\text{plankters present}}{\text{m}^2} \times 100 = \text{predation pressure}$

Predation pressure is defined as the percent of zooplankton removed per day. Table 10 shows the combined monthly predation pressure in Lakes Anderson-Cue and McCloud during 1969-1970. The values of predation pressure were usually less than 1.0 percent, except for *C. sphaericus* in February, 1970 (3.56 percent).

TABLE 10

Monthly Predation Pressure by E. fusiforme and H. formosa in Lakes
Anderson-Cue (A-Q) and McCloud (McC), 1969-1970.

Organism		Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
<u>A. curvirostris</u>	A-Q				+			0.24	+	+
	McC						+	0.68	0.025	+
<u>A. harpae</u>	A-Q	0.05	0.05	0.10	+	+	0.11	0.59	0.62	0.17
	McC						+	+		
<u>A. quadrangularis</u>	A-Q	0.008	0.03	0.08	0.058	0.01	0.04	0.52	0.49	+
	McC	0.20	0.35	0.038	0.12	0.01	0.05	0.09	0.087	0.107
<u>C. piger</u>	A-Q		0.04	0.01			+			+
	McC	0.08	0.02	0.24	0.002	+	+	0.10	0.045	0.25
<u>C. sphaericus</u>	A-Q	0.08		0.09	0.19	0.49	0.36	0.82	3.56	0.13
	McC		+			0.43	0.37	0.20	0.05	0.36
<u>G. testudinaria</u>	A-Q	+	+	++	0.10	0.012	0.072	0.08	+	+
	McC		0.89				0.01	+	0.024	+
<u>I. spinifer</u>	A-Q	0.09	0.05	0.10						
	McC		+		0.008	+		0.044		
<u>M. rosea</u>	A-Q	0.12	0.64	++	0.25	++	+	+		
	McC		++		+			+		
<u>P. striatus</u>	A-Q	0.006	0.02		0.008	0.027	0.24	+	0.02	
	McC	+	0.03					0.02	0.014	+
<u>S. exspinosus</u>	A-Q	0.34	0.93	0.22	0.28	+	+			
	McC	0.03	0.17	+	+		+	0.24	+	+
<u>Lecane spp.</u>	A-Q	0.021	0.31	0.07	0.17	+	0.105			
	McC	0.52	0.21	0.10	0.17	0.01	0.12	0.05	0.014	0.016
<u>Monostyla sp.</u>	A-Q	0.08	0.054	0.08	0.41		0.007			
	McC	0.63	0.14	0.09	0.23		0.16	0.06	0.006	0.02
Copepoda	A-Q	0.04	0.05	0.04	0.03	0.033	0.006	0.03	0.01	0.007
	McC	0.05	0.16	0.003	0.024	0.016	0.03	0.04	0.018	0.032

+ = eaten, but not present in plankton sample.

++ = large quantity eaten, but not present in plankton sample.

DISCUSSION

Population Dynamics and Species Diversity

Relative to the limnetic zone, the littoral is subject to drastic seasonal fluctuations in temperature and water level. Algal primary productivity fluctuations are probably similar to those in the limnetic zone. According to Straškraba (1963), the littoral herbivores are dependent on limnetic primary production because littoral primary production due to phytoplankton and periphyton is not sufficient to maintain the high herbivore production.

The monovariate correlations showed that no single environmental variable was responsible for population fluctuations in all groups. From the multiple regression and correlation analysis on groups which were present all year, temperature was an important factor to C. sphaericus populations and primary productivity to Lecane spp. populations.

The effects of primary productivity and temperature on Daphnia populations have been studied by Hall (1964). He found that the number of eggs per brood and the amount of growth per instar were unaffected by temperature, but positively correlated with food supply. However, the average length of an instar was dependent on temperature. Thus the rate of reproduction was dependent on both factors.

Hutchinson (1967) observed that a common feature of limnetic zooplankton populations was the occurrence of low populations in late winter,

usually under ice. He suggested that the rise in both phytoplankton and temperature in the spring would be conducive to an increase in cladoceran populations.

Since Cladocera and Rotifera life cycles are similar, primary productivity and temperature would be correlated with the rate of reproduction, and thus, changes in population densities of both groups.

In the multiple regression analyses Copepoda were not highly correlated with the three environmental parameters. According to Hutchinson (1967), variations in copepod egg number are less clearly associated with environmental conditions than in Cladocera. Also, the immature stages of the life cycle presumably give copepods a greater range of filtrable food, thus making them more adjustable to varying conditions than Cladocera.

Ward (1940) reported that temperature was the most important single physical factor in controlling entomostracan populations in Ohio ponds. During her study, populations of C. sphaericus were present all year in deeper ponds, but disappeared in shallow ponds during the winter.

Both Anderson-Cue and McCloud had their highest density of Cladocera in the summer, 1968 (Figures 1, 3), corresponding to high primary productivity (Figure 7). While both showed a decreased density in the fall, Anderson-Cue had a high density of Cladocera from December through February and McCloud maintained low populations. This accompanied a high primary productivity.

Primary productivity in the two lakes was significantly correlated ($r = 0.511$, $p = 0.01$) in 1968-1969. However, in 1969-1970, this correlation was higher ($r = 0.907$, $p = 0.001$), indicating a greater similarity between the lakes.

In 1969-1970 both lakes again had high summer cladoceran populations and decreasing fall populations (Figures 2, 4). Differences between cladoceran densities were probably due to an interaction between environmental parameters. Decreasing primary productivity and temperature and habitat changes due to increasing lake level resulted in a decrease in population density in both lakes in the fall. However, the greater abundance of C. sphaericus in McCloud than in Anderson-Cue from January through March, 1970, suggests that the better developed littoral zone of McCloud was not as strongly affected by lake level fluctuations. Benthic and vegetation inhabiting species had decreased population densities in both lakes.

The lowered species diversity (Table 4) and abundance of littoral zooplankton in the fall (Figures 1 - 6) could have been caused by three factors. Temperature (Figure 8) was dropping through this period both years. However, it was lowest during December through February and did not exceed the December average until March. By January the species diversity and abundance had increased. All groups were generally numerous at peaks in temperature (July - August).

Primary productivity (Figure 7) was also dropping or low during the fall. However, its average value September through December was not lower than January through May. Peaks in abundance of all groups corresponded to peaks in primary productivity. Primary productivity was highly correlated with temperature and was thus low January through March, although species diversity returned to a high value in Lake McCloud in the spring. Anderson-Cue had a high primary productivity and species diversity in the spring of 1969.

Lake level (Figure 8) rose drastically at the end of August, 1968, was high September through December, started dropping in December and steadily dropped through May, 1969. It began to rise again in July and by the end of August was over one foot higher than the level for August, 1968. It continued to rise throughout the year. Sampling depth was kept constant throughout the study. Consequently, vegetation in the sampling area was reduced in the fall due to the rapid increase in lake level, slow macrophyte growth and delayed aufwuchs colonization. The continued increase in lake level might also have been responsible for the lower values of primary productivity in both lakes in the spring of 1970 compared to the spring of 1969. The pattern of species diversity was best related to the changes in lake level, since diversity was low as lake level increased and was high when lake level stabilized or was dropping.

The littoral vegetation is the most suitable habitat for most of the Chydoridae (Whiteside, 1970). The species which were absent or had lower population densities in the spring of 1970 compared to the spring of 1969 were A. rectangula, A. guttata, A. costata, C. rectirostris and A. globulosa. These species inhabit the littoral vegetation (Table 11) and would be most affected by the increasing lake level.

Of the three predominant species in Anderson-Cue during the fall of 1968, A. quadrangularis inhabits the sediment-water interface and C. sphaericus is commonly limnetic. Consequently, they would not be strongly affected by the decrease in littoral vegetation. In Lake McCloud, A. quadrangularis was the dominant species in the fall.

Of the nine predominant species in McCloud during October through January of 1969-1970, five were rotifers and two were copepods. The two species of Cladocera were C. sphaericus and A. quadrangularis. January through

March, the species diversity increased, but the zooplankton included species commonly found in the limnetic zone, such as B. coregoni, Keratella spp. and Conochiloides sp., which had not been present the previous summer.

The species diversity in Anderson-Cue remained low in the spring, 1970. From January through March, populations of all chydorids were reduced, but B. coregoni, Rotifera, especially Keratella spp., and Copepoda had high densities.

Thus, it appears that temperature and primary productivity affected abundance of littoral zooplankton most of the year. During the fall, the abundance of several species, as well as diversity, was most strongly influenced by the effect of lake level changes on the littoral vegetation.

In their studies of cladoceran microfossils, Harmsworth and Whiteside (1968) suggested that the dominant factor influencing the abundance and diversity of chydorids was the extent of the littoral. They concluded that the production of chydorids must in some way be related to the nature of the shallow-water substratum and its associated plants and animals. Smyly (1958) reported that the distribution of many species was correlated more closely with the presence of aquatic weeds or the character of the bottom than with the chemistry of the water. Armitage and Davis (1967) observed that the relative abundance of Cladocera was related to the development of rooted vegetation. Quade (1969) found some evidence of associations of littoral Cladocera with aquatic macrophytes. Whiteside's data (1970) suggested that species diversity is a function of available habitat and, thus the distribution of most chydorid species within a region is determined by habitat diversity.

Certainly in these sandhills lakes, the factors of temperature, primary productivity, water level and amount of vegetation were interrelated. However, the littoral vegetation at the sampling site, and thus habitat, varied most directly with lake level.

Prey Selection

Cladocera were the most important items in the diet of both fishes (Figures 9 - 20). Energetically, this seems reasonable, since littoral Cladocera are poor swimmers compared to copepods and would be easier to capture. Because of their small size, rotifers would be energetically important food sources only when numerous.

When Cladocera were scarce, E. fusiforme consumed copepods and nonplankton, while H. formosa ate mainly rotifers and some nonplankton. Rotifers were a large component of the diet even when they were not abundant.

In Anderson-Cue E. fusiforme had a mean electivity index of -0.43 for copepods, while H. formosa had a value of -0.49. In McCloud the mean electivity index of E. fusiforme was +0.12 and that of H. formosa was -0.28. This implies that E. fusiforme was somewhat better at obtaining copepods than H. formosa, but they were not highly selected by either fish. Also E. fusiforme in McCloud was dependent on copepods for a longer time than in Anderson-Cue, due to the lower cladoceran populations.

Nonplankton was apparently not as abundant in Anderson-Cue as in McCloud, since it did not constitute a large part of the diet of either fish in Anderson-Cue.

As evident from the low levels of predation pressure (Table 10), the two fishes had an abundant food supply when Cladocera were numerous.

TABLE 11

Mean Length and Microhabitat of Common Species of Littoral Zooplankton.

Organism	Mean Length (μ)	Microhabitat
<u>A. curvirostris</u>	940	Aquatic weeds in shallow water ^{1,4}
<u>A. harpae</u>	635	Weeds and open water ^{1,6}
<u>A. affinis</u>	730	Benthic, in littoral ^{1,2,3,4,5,6}
<u>A. guttata</u>	280	Weeds ¹ , muddy bottoms ^{5,6}
<u>A. quadrangularis</u>	700	Benthic, in littoral ^{1,2,3,4,5,6}
<u>A. globulosa</u>	310	Weeds, in littoral ⁴
<u>C. rectirostris</u>	540	Weeds ^{1,4,5,6} , benthic ²
<u>C. piger</u>	310	Weeds and benthic ^{1,5,6}
<u>C. sphaericus</u>	250	Weeds and open water ^{3,5,6}
<u>G. testudinaria</u>	570	Weeds ^{4,5,6} , benthic ^{1,4,5}
<u>I. spinifer</u>	700	Weeds ⁴ , benthic ^{4,5}
<u>M. rosea</u>	540	Weeds ⁴
<u>P. striatus</u>	305	Weeds ⁴
<u>S. exspinosus</u>	1530	Weeds and open water ⁴

1. Smyly, 1958
2. Cole, 1955
3. DeCosta, 1968
4. Brooks, 1959
5. Whiteside, 1970
6. Fryer, 1968

Because of partitioning of resources when Cladocera were scarce, competition did not occur. The period when their feeding habits were most similar (when their niches overlapped) was when food supply was not limiting.

The preference of small fishes for Cladocera has been found by other workers. McLane (1948) reported that young largemouth bass fed to a large extent on Cladocera. They were more important than copepods in the diet. Gerking (1964) found that Cladocera were twice as numerous in the stomachs of bluegill sunfish as amphipods, ostracods or copepods. A change in the diet to midges was correlated with the collapse of Daphnia populations. Nikolsky (1963) listed Rotifera and microcrustacea as basic food for young fishes. Brooks (1969) mentioned that planktivorous fishes prefer Cladocera to calanoid copepods of the same size.

Prey selection appeared to be determined by a combination of factors. Both fishes had high mean electivity indices for the same species of Cladocera. These were generally large and/or benthic species (Table 11). E. fusiforme always had higher mean electivity indices for the benthic species than H. formosa. H. formosa had higher indices for the smaller vegetation inhabiting species, but these were usually negative. Mean indices for C. sphaericus were similar, indicating an equal availability.

If the average percent of the diet made up by each cladoceran species is examined (Table 8), the results are similar. The large benthic species averaged 5.0 percent of the diet of E. fusiforme and 2.4 percent of the diet of H. formosa. Small species which inhabit the vegetation constituted 0.9 percent of the diet of E. fusiforme and 1.6 percent of the diet of H. formosa. Thus, the large benthic species were more important to both fishes than the small vegetation inhabiting species.

Size and accessibility seemed to be equally important factors in food selection. Accessibility refers to the behavior of the prey, such as concealment or ease of escape. It also refers to characteristics of the predator which equip it for catching certain prey. This is similar to the definition of Ivlev (1961), although he considers accessibility to be more a property of the prey. To a slight extent, size is a component of accessibility, since larger plankters are usually better swimmers. Also, an organism may be too large or too small to be eaten. In this case all organisms studied were within a suitable size range for both fishes.

Large benthic Cladocera were selected by both fishes over small species. However, since E. fusiforme rests on the bottom, these Cladocera may be more accessible, which would explain higher electivity indices. Among the Rotifera and Copepoda, accessibility seemed to be more important than size. H. formosa selected Rotifera over Copepoda, perhaps because it was not as efficient as E. fusiforme at catching copepods.

Abundance, of course, plays some role. If an organism is so rare that it is seldom encountered, it would not seem to be energetically important. However, small Cladocera were negatively selected despite their abundance and large Cladocera constituted sizeable portions of the diet even when scarce. Thus, abundance was not a significant factor in prey selection.

Studies on food selection in pelagic fishes showed size to be the most important factor. Brooks and Dodson (1965) reported that predation by the alewife eliminated large zooplankters. They mentioned that size, abundance, edibility and ease of capture were bases for food selection, with size being most significant. Galbraith (1967) looked at the

relationship of the size frequency of Daphnia in the plankton to that in rainbow trout and yellow perch stomachs. In spite of the fact that 46 percent of Daphnia in the lake consisted of smaller individuals, 96 percent of those eaten by trout and 82 percent by perch were larger than 1.3 mm. An examination of gill rakers showed that a large fraction of the spacings were small enough to filter out plankters less than 1.3 mm. Houde (1967) found that density of zooplankton was not an important factor controlling the amount eaten by walleye fry. Using Ivlev's method for calculating electivity indices, he found a slightly positive selection for total copepods. Genera of large copepods had higher values than smaller ones. Cladocera were always negatively selected. His data indicated that size was not the only factor controlling food selection, since walleye fry did not eat Diaptomus, but ate Cyclops, a smaller copepod. Houde suggested that Diaptomus might have been able to avoid the fry. Data by Galbraith (1967) and Dodson (1970) suggested that size-selective predation can result in a greater diversity of predators by increasing the number of feeding specialties.

Thus, studies of pelagic fishes have shown that size is the most important factor determining prey selection in the limnetic zone. Since neither fish nor zooplankton habitats are as well defined in the limnetic zone as in the littoral, it seems logical that the importance of accessibility would be reduced.

Predation Pressure

The feeding of E. fusiforme and H. formosa on the littoral zooplankton is only a small part of the total predation. All of the littoral fishes feed to some extent on them. Also, species of game fish and pelagic

fishes spend a portion of their lives in the littoral. Bluegill fry, in particular, feed heavily on littoral Cladocera in these lakes (personal observations).

The values of predation pressure (Table 10) were usually low. The highest value was on C. sphaericus, 3.56 percent, in February, 1970. Dodson (1970) measured removal rates of Daphnia due to salamander and midge larvae predation in a similar fashion. When his values are expressed as percent removed per day, they are of the same order of magnitude as my values for C. sphaericus. Hall (1964) estimated total predation pressure on Daphnia in the summer to be 21.9 percent per day. He concluded that predation was the most important factor controlling population size in the summer.

The fact that gut clearance rate increases with temperature and that fish densities are greatest in the summer indicates a greater predation in the summer, which corresponds to the time of highest number of species and abundance of littoral zooplankton. This strengthens the observation that the littoral zooplankton are not controlled by E. fusiforme and H. formosa. However, bluegill fry enter the littoral in late August from the limnetic zone. Since this is a time of decreasing zooplankton populations, they may exert a much stronger predation pressure.

The effect of predation on prey populations has been examined. Slobodkin (1961) speculated that where two species are limited by predation, they can coexist if they differ from each other ecologically to some significant degree. The stability of a system is increased by ecological diversification of the species. Connell (1961) found that predation tended to decrease competition between two species of barnacles.

Paine (1966) suggested that animal species diversity is related to the number of predators in a system and their efficiency in preventing single species from monopolizing some limiting resource.

Since many species of littoral zooplankton are approximately the same size and utilize the same food supply, they would compete when these resources were limiting. By keeping prey species populations below the level of resource limitation, predation could play an important role in maintaining a high species diversity.

Eutrophication

It was difficult to demonstrate a cause-effect relationship between changes in littoral zooplankton and enrichment of Lake Anderson-Cue.

Brooks (1969) mentioned that an increase in standing crop of herbivores was an expected consequence of enrichment. The total zooplankton was generally greater in Anderson-Cue than in McCloud. However, a decrease in abundance was seen in both lakes the second sampling year. Changes in abundance, species composition and diversity were more likely correlated with changes in the littoral zone as a result of lake level fluctuations than with enrichment.

Whiteside and Harmsworth (1967) found a high correlation between transparency and species diversity in Danish and Indiana lakes. Since chydorids are typically inhabitants of the macrophytic vegetation, they suggest that this habitat extends to greater depths in clearer lakes. Lesser penetration of light in more enriched lakes due to phytoplankton blooms and dissolved organic matter would decrease habitat diversity and thus, species diversity. Whiteside (1970) divided the chydorid associations into three areas: the littoral vegetational, the littoral benthonic and the limnetic. He found that in lakes of extreme eutrophy,

limnetic species (*C. sphaericus*, *A. rectangula*) comprised most of the chydorids. The benthic species were not as much affected by eutrophication as those which inhabited the littoral vegetation.

Changes in habitat diversity can occur as a result of long-term phenomena, such as eutrophication, or short-term phenomena, such as lake level fluctuations. Both would have similar effects on diversity and density of littoral zooplankton. Also, changes in the composition of zooplankton may result from selective predation. In order to use littoral zooplankters as indicators of eutrophication, the effects of changes in environmental parameters, as well as selective predation, on the population dynamics of littoral zooplankters must be understood.

The effects of environmental variables on littoral zooplankton populations are complex. Because of their effect on the rate of reproduction, primary productivity and temperature are probably the most important controlling factors. However, the correlations between population and density and primary productivity could be improved if the contribution of periphyton were considered. According to Fryer (1968), periphyton is an important food source for several species of Chydoridae.

This and earlier studies have shown that changes in habitat diversity affect population density, as well as diversity of littoral zooplankton. Although lake level fluctuations were monitored, this did not give an adequate reflection of changes in the littoral zone. To determine the effects of eutrophication on littoral zooplankton, quantitative measurements of changes in macrophytes and aufwuchs are needed, since these would be more indicative of changes in habitat diversity.

Predation by E. fusiforme and H. formosa does not appear to control population densities of littoral zooplankters in these lakes. However, a measure of total predation might show this to be an important factor, especially when game fish fry are present in the littoral zone.

SUMMARY

In this study the effect of environmental factors on the interaction of littoral zooplankton and their fish predators was examined. The most important conclusions were

1. Of the environmental parameters examined, fluctuations in primary productivity and temperature had the greatest effect on littoral zooplankton abundance.
2. Fluctuations in lake level and the resultant effects on vegetation in the littoral had the greatest influence on species diversity.
3. Littoral Cladocera were the most important food items for E. fusiforme and H. formosa.
4. When littoral Cladocera were scarce, E. fusiforme fed mainly on Copepoda and nonplankton, while H. formosa chiefly ate rotifers.
5. Food selection was determined by size and accessibility of prey.
6. Predation pressure by E. fusiforme and H. formosa was not great enough to be an important factor controlling littoral zooplankton populations.
7. Changes in species composition and diversity were more likely correlated with changes in the littoral zone as a result of lake level fluctuations than with eutrophication.
8. Attempts to use littoral zooplankton as indicators of lake trophic state must differentiate between transient fluctuations induced by seasonal or lake level changes and eutrophication effects.

LITERATURE CITED

- Armitage, K. B., and M. Davis, 1967. Population structure of some pond microcrustacea. *Hydrobiologica* 29: 205-225.
- Berg, A., and E. Grimaldi, 1966b. Ecological relationships between fish species in the Lago Maggiore. *Verh. Int. Ver. Limnol.* 16: 1065-1073.
- Birge, E. A., 1910. Notes on Cladocera IV. Descriptions of new and rare species chiefly southern. *Trans. Wisconsin Acad. Sci.* 16: 1018-1066.
- Brezonik, P. L., W. H. Morgon, E. E. Shannon and H. D. Putnam, 1969. Eutrophication factors in north central lakes. Engineering and Industrial Experiment Station, Bull. Ser. No. 134, Water Resources Research Center Publ. No. 5.
- Brooks, J. L., 1959. Cladocera. Fresh-water biology, W. T. Edmondson (ed.) John Wiley and Sons, Inc., New York. 1248 pp.
- , 1968. The effects of prey-size selection by lake planktivores. *Syst. Zool.* 17: 272-291.
- , 1969. Eutrophication and changes in the composition of the zooplankton. Symposium on eutrophication: causes, consequences, correctives. *Nat. Acad. Sci., Washington, D. C.*
- , and S. I. Dodson, 1965. Predation, body size and composition of plankton. *Science* 150: 28-35.
- Chable, A. C., 1947. A study of the food habits and ecological relationships of the sunfishes of northern Florida. Master's thesis, University of Florida, Gainesville, Florida.
- Cole, G. A., 1955. An ecological study of the microbenthic fauna of two Minnesota lakes. *Amer. Midl. Nat.* 53: 213-230.
- Connell, J. H., 1961. The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. *Ecology* 42: 710-723.
- DeCosta, J., 1964. Latitudinal distribution of chydorid Cladocera in the Mississippi Valley based on their remains in surficial lake sediments. *Invest. Indiana Lakes and Streams* 6: 65-101.
- , 1968. The history of the chydorid community of a small lake in Wind River Mountains, Wyoming, U. S. A. *Arch. Hydrobiol.* 64: 400-425.

- Dodson, S. I., 1970. Complementary feeding niches sustained by size-selective predation. *Limnol. Oceanog.* 15: 131-137.
- Frey, D. G., 1961. Developmental history of Schleinsee. *Verh. Int. Ver. Limnol.* 14: 271-278.
- Fryer, G., 1968. Evolution and adaptive radiation in the Chydoridae (Crustacea: Cladocera): a study in comparative functional morphology and ecology. *Phil. Tran. Royal Soc., Series B*, 254: 221-385.
- Galbraith, M. G., 1967. Size-selective predation on Daphnia by rainbow trout and yellow perch. *Trans. Am. Fisheries Soc.* 96: 1-10.
- Gerking, S. D., 1964. Timing and magnitude of the production of a bluegill sunfish population and its food supply. *Verh. Int. Ver. Limnol.* 15: 496-503.
- Goulden, C. E., 1964. The history of the cladocera fauna of Esthwaite Water and its limnological significance. *Arch. Hydrobiol.* 60: 1-52.
- Hall, D. J., 1964. An experimental approach to the dynamics of a natural population of Daphnia galeata Mendotae. *Ecology* 45: 94-112.
- Hansen, Kaj., 1961. Lake types and lake sediments. *Verh. Int. Ver. Limnol.* 14: 285-290.
- Harmsworth, R. V., 1968. The developmental history of Blelham Tarn (England) as shown by animal microfossils, with special reference to the cladocera. *Ecol. Monog.* 38: 223-241.
- , and M. C. Whiteside., 1968. Relation of cladoceran remains in lake sediments to primary productivity of lakes. *Ecology* 49: 998-1000.
- Houde, E. D., 1967. Food of pelagic young of the walleye, Stizostedion vitreum, in Oneida Lake, New York. *Trans. Am. Fisheries Soc.* 96: 17-24.
- Hutchinson, G. E., 1967. A treatise on limnology. Vol. II. Introduction to lake biology and the limnoplankton. John Wiley and Sons, Inc., New York. 1115 pp.
- Ivlev, V. S., 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, Connecticut. 302 pp.
- Lee, G. F. (Chairman), 1966. Report on the nutrient sources of Lake Mendota. Nutrient Sources Subcommittee of the Lake Mendota Problems Committee, Madison, Wisconsin. (Mimeo, 41 pp.)
- Margalef, R., 1963. On certain unifying principles in ecology. *The Amer. Nat.* 97: 357-374.

- Maslin, P. E., 1969. Population dynamics and productivity of two sandhills lakes. Ph.D. dissertation, University of Florida, Gainesville, Florida.
- McLane, W. M., 1948. The seasonal food of the largemouth black bass, *M. salmoides floridanus* in the St. Johns River, Welaka, Florida. Quart. Journ. Florida Acad. Sci. 12: 195-201.
- , 1955. The fishes of the St. Johns River system. Ph.D. dissertation, University of Florida, Gainesville, Florida.
- Mueller, W. P., 1964. The distribution of cladoceran remains in surficial sediments from three northern Indiana lakes. Invest. Indiana Lakes and Streams 6: 1-63.
- Nikolsky, G. V., 1963. The ecology of fishes. Acad. Press, New York. 352 pp.
- Paine, R. T., 1966. Food web complexity and species diversity. Amer. Nat. 100: 65-75.
- Pennak, R. W., 1955. Persistent changes in the dominant species composition of limnetic entomostracan populations in a Colorado mountain lake. Trans. Am. Microsc. Soc. 74: 116-118.
- Quade, H. W., 1969. Cladoceran faunas associated with aquatic macrophytes in some lakes in Northwestern Minnesota. Ecology 50: 170-179.
- Shannon, C. E., 1949. The mathematical theory of communication. Univ. Ill. Press, Urbana, Illinois.
- Slobodkin, L. B., 1961. Growth and regulation of animal populations. Holt, Rinehart and Winston, Inc., New York.
- Smyly, W. J. P., 1957. Distribution and seasonal abundance of entomostraca in moorland ponds near Windermere. Hydrobiologia 11: 59-72.
- , 1958. The cladocera and copepoda (Crustacea) of the tarns of the English lake district. J. Anim. Ecol. 27: 87-103.
- Straškraba, M., 1963. Contributions to the productivity of the littoral region of pools and ponds. 1. Quantitative study of littoral zooplankton of the rich vegetation of the backwater Labičko. Hydrobiologica 26: 421-443.
- Ward, E. B., 1940. A seasonal study of pond entomostraca in the Cincinnati region. Amer. Midl. Nat. 23: 635-691.
- Whiteside, M. C., 1968. Chydorid (Cladocera) remains in surficial sediments of Danish lakes and their significance to paleolimnological interpretations. Symposium on Paleolimnology, D. G. Frey, ed. Mitt. Int. Ver. Limnol. No. 17.

Whiteside, M. C., 1970. Danish chydorid cladocera: modern ecology and core studies. Ecol. Monog. 40: 79-118.

-----, and R. V. Harmsworth, 1967. Species diversity in chydorid (Cladocera) communities. Ecology 48: 664-667.

BIOGRAPHICAL SKETCH

Karolyn R. Maslin was born January 28, 1947, in Fayetteville, North Carolina. She attended Severna Park High School, Maryland. In September, 1964, she entered the University of Florida from which she received the Bachelor of Science degree in 1967. In January, 1968, she began graduate work in the Department of Zoology at the University of Florida. She received a traineeship grant through the Department of Environmental Engineering. In July, 1969, she was granted permission to bypass the master's degree and has since pursued work toward the degree of Doctor of Philosophy. She received a research fellowship grant from the Federal Water Pollution Control Administration to finance her last year of graduate work.

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This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of that committee. It was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council, and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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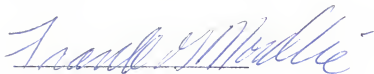
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